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MALIA, DOCODONTA)

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ABSTRACT

The pattern of molar occlusion in the Late Jurassic mammal genus *Docodon* was determined by "mapping" the wear facets on all known upper and lower dentitions. The coincidence of lower and upper molar wear is evidence that the proposed occlusal pattern is correct. The lingual halves of the upper molars occlude in the lower intermolar basins formed by the adjacent halves of lower molars. The buccal halves of upper molars pass buccally to the lower molar row. The disposition of opposing cusps and crests, and the verticality of most wear facets, reveals that molar function was primarily shearing rather than crushing. The vertical crenelations (or ribs and furrows) on the molar crowns are interpreted as accessory shearing edges.

INTRODUCTION

The genus *Docodon* is one of the Mesozoic mammalian genera named by Marsh (1880 and later papers) from material collected at Como Bluff, Wyoming. The order Docodonta (to which *Docodon* belongs) is known chiefly from the dentition and on this evidence is generally considered to be too specialized to have been closely related to therian ancestors. This paper provides a functional evaluation of occlusion in *Docodon,* and presents other conclusions on cusp homology and molar function. Previous accounts and diagrams of molar occlusion in *Docodon* (Simpson, 1929: 71; 1933: 145; Patterson, 1956: 73; Butler, 1961: 123; Vandebroek, 1961: 281) differ in detail and leave considerable doubt as to the precise occlusal relationship of upper and lower molars. The descriptions of *Docodon* molars given by Simpson (1929), Butler (1939) and Patterson (1956) obviate the necessity of redescribing the molars. A representative upper and lower molar are here fully illustrated for the first time (Figs. 5-14). Certain questions of taxonomy and cusp nomenclature will be discussed as they relate to the reconstruction of the occlusal pattern.

MATERIALS

All available specimens of *Docodon* were studied. These specimens are housed in the Peabody Museum of Natural History, Yale University (YPM), the U. S. National Museum (USNM) and the American Museum of Natural History (AMNH). *Docodon* is known from only two localities, both in the Morrison Formation: the "Old Quarry" at Garden Park, Fremont County, Colorado, and Quarries 9 and 1 at Como Bluff, Albany County, Wyoming. The Garden Park material consists of two specimens, USNM 21863 and USNM 2717, which on the basis of present knowledge cannot be assigned to any species known from Quarry 9. A single lower jaw (AMNH 3002) was recovered from Quarry 1 at Como Bluff; the remaining 58 specimens come from Quarry 9.

TAXONOMIC CONSIDERATIONS

Five species of *Docodon* were recognized by Simpson (1929). Of these, four are based on partial or nearly complete mandibles: *D. victor* (Marsh 1880), *D. striatus* Marsh 1881, *D. crassus*

(Marsh 1887) and *D. affinis* (Marsh 1887). The fifth species, *D. superus* Simpson, 1929, is a conventional species for all upper dentitions of this genus.

No associated upper and lower dentition of *Docodon* is yet known and no criteria have been recognized by which species based on lower dentitions can be confidently related to any upper dentitions. Partly for these reasons and partly on account of the lack of variation in available material did Simpson (1929) place all upper dentitions of *Docodon* in a separate species. The unsatisfactory state of knowledge of *Docodon* species may tend to cast doubt on any reconstruction of the occlusion. Furthermore, of the 23 specimens of lower dentitions that are sufficiently well preserved to be utilized in this study, only five (including the four type specimens) could be identified to species; the other fragmentary specimens could only be referred to *Docodon* sp. because the species diagnoses are based on more or less complete mandibles with most of the alveoli if not nearly all of the teeth present. There are reasons to believe, however, that there are actually fewer species. Simpson (1929: 86-87) pointed out that the only difference between the type specimens of *D. striatus* and *D. victor* lay in the molar number, the former having seven and the latter eight, and that this difference could well be due to the immaturity of the type of *D. striatus*. Inasmuch as the type is the only assigned specimen of the species, and complete lower dentitions are so few, it is also possible that *Docodon* molars varied in number within a species. Although Simpson recognized this possibility as the most plausible, he nonetheless deemed it "best to retain Marsh's species provisionally" (1929: 87). A strong case has yet to be made for this species distinction, and the present study of all material failed to reveal any taxonomically significant differences.

Similar arguments may be made for synonymizing both *Docodon crassus* with *D. affinis* and *D. striatus*. The principal features that distinguish *D. crassus* from *D. affinis* and *D. striatus* (P_3, M_6, and a shorter and more shallow jaw) are probably due to the immature condition of the types. Characteristics that separate them from each other are based on the relative sizes of P_3, P_4, and the canines, and on minor differences in the premolar external cingula. Referring to *D. crassus* and *D. affinis*, Simpson (1929: 89) wrote: "They do have some slight differences from the other species now

referred to this genus, but these are so unimportant, and even doubtful, that their real validity can only be tested by a still larger series of specimens than is now available. It is probable that *Docodon* includes more than one species, and perhaps as many as four or five but one must hesitate to vouch for the necessary validity of all the present established species."

A taxonomic revision awaits new and more complete material and is not the purpose of this paper. The four species based on lower dentitions and the one conventional species created for upper dentitions, although nominally separate, may in fact be regarded as one for purposes of determining the occlusal pattern and function of the dentition as presently known. No important variations in molar cusp pattern or crown morphology were detected during the present study of *Docodon* material. Observed differences in wear facet development are slight and are apparently the result of variable degree of wear or of minor variations in occlusion, neither of which is admissible as a taxonomic character.

Cusp Homology and Molar Morphology

CUSP HOMOLOGY. Simpson (1929), Butler (1939) and Patterson (1956) designated the largest buccal cusp on *Docodon* upper and lower molars as the paracone and protoconid, respectively. These cusps almost certainly represent the primary cusps of reptilian ancestry. Crompton and Jenkins (1968) employed the letters *A* and *a* in referring to these cusps; this approach facilitated comparisons among non-therian teeth without employing terminology usually used for therian teeth. However, it is clear from that study and from those of other workers that the paracone and protoconid of docodonts are homologous with the similarly named cusps of therians.

The homology of other cusps is not so easily established. Simpson's (1929) and Butler's (1939) descriptions use a tribosphenic terminology, in keeping with the then current belief that docodonts were aberrant pantotheres. Gidley (1906) was the first to propose that the docodont dentition was derived from an evolutionary lineage apart from that leading to the tribosphenic pattern. Later, Patterson (1956) presented a concrete outline of docodont-eozostrodont (=morganucodont) relationships. Sub-

sequently, Crompton and Jenkins (1968) documented Patterson's proposed phylogeny in more detail, using wear-facet evolution and the dental structure of the docodont *Haldanodon*[1] as evidence. The argument that only the docodont protoconid and paracone have homologues among therian dentitions, as claimed by Patterson (1956), is based on the supposition that the common ancestor of docodonts and therians had a haplodont dentition. However, Crompton and Jenkins (1968) pointed out that cynodonts, which were the precursors of most Triassic and later Mezozoic mammals, already had a tricuspid dentition. Furthermore, Crompton and Jenkins hypothesized that the common ancestor of both therians and docodonts may have been an early eozostrodontid with a molar pattern like that of *Eozostrodon*. Thus, if both docodonts and therians are derived from an ancestor with a basically tricuspid dentition, more than one cusp on each upper and lower molar may be homologous.

The evolution of the docodont molar from the eozostrodont molar involved two basic modifications: (1) lingual expansion of both upper and lower molar crowns, and (2) loss of one primary cusp on each lower and upper molar. The lingual expansion involved new or otherwise displaced cusps that cannot be compared with any cusps in the tribosphenic lineage. Modification of the buccal aspect of the molars is not so great. As Patterson first noted, loss of the cusps immediately posterior to the protoconid (cusp *c*, Fig. 1) and anterior to the paracone (cusp *a*, Fig. 1)[2] transforms an eozostrodontid pattern into a docodont pattern. Two cusps of the original cynodont tricuspid pattern remain: on the lower molar, the protoconid and the cusp anterior to it (cusp *a*), and on the upper molar, the paracone and the cusp posterior to it (cusp *c*). Inasmuch as the tricuspid molar pattern is basic to both therian and non-therian (i.e., triconodont, docodont) dentitions, then it is probable that lower cusp *a* is the paraconid and upper cusp *c* is the metacone. However, use of these terms seems unwarranted at present because they connote derivation from a tribosphenic pattern. As an alternative, Patterson's (1956) terminology

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[1] *Haldanodon* is a *nomen nudum* because Kühne (1968) failed to designate any species for this genus. Anticipating that this taxonomic problem will be resolved, I use this name for the Kimmeridgean docodonts from Portugal described by Kühne (1968).

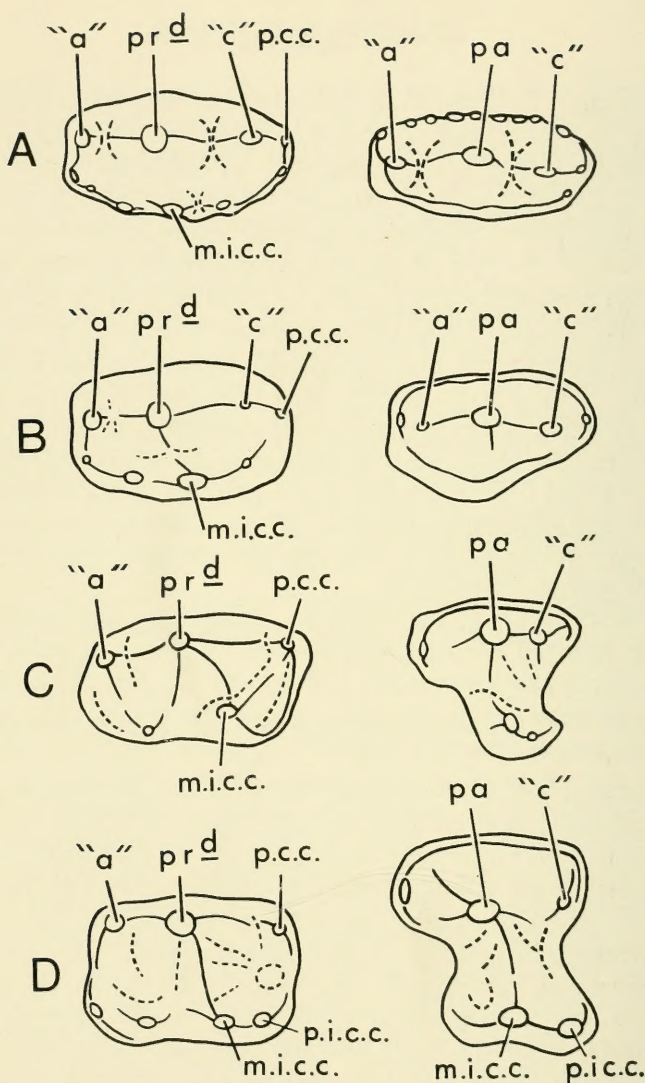[2] Crompton and Jenkins (1968) referred to upper cusp *a* as cusp *B*.

FIG. 1. Molar evolution and cusp homologies in the teeth of Triassic eozostrodontids and Jurassic docodonts. A) *Eozostrodon,* from the Rhaetic; after Crompton and Jenkins, 1968. B) Hypothetical Early or Middle Jurassic docodont. C) *Haldanodon,* from sediments of Kimmeridgean age, Portugal; after Kühne, 1968. D) *Docodon,* from the Late Jurassic Morrison Formation. On the left are lower molars, on the right, upper molars. Anterior is to the left; lingual aspect toward the bottom of the page. Not drawn to scale. Abbreviations: "a"—cusp *a;* a.c.c.—anterior cingulum cusp; a.i.c.c.—antero-internal cingulum cusp; "c"—cusp *c;* d.c.—distal cuspule; m.i.c.c.—main internal cingulum cusp; pa—paracone; p.c.c.— posterior cingulum cusp; p.i.c.c.—postero-internal cingulum cusp; prd— protoconid.

is available; in the interest of providing designations that are free from the tribosphenic context, and to avoid erecting a new terminology, Patterson's terminology is used in this paper.

MOLAR MORPHOLOGY. The rectangular lower molars progressively increase in crown length and width from M_1 to M_5 (Fig. 2B). M_6 is slightly smaller in both dimensions than the preceding molar, and its nearly rectangular shape contrasts to all other molars in which the posterior width is somewhat greater than the anterior width. These minor differences aside, the pattern and relative proportions of the cusps remain so constant throughout the molar series that the details of a single molar may be taken as representative (Figs. 5-9). The maximum lengths and widths in millimeters of the molars of the holotype of *Docodon victor,* YPM 11826, are respectively: M_1, 1.64, 1.18; M_2, 2.02, 1.22; M_3, 2.14, 1.47; M_4, 2.18, 1.51; M_5, 2.22, 1.64; M_6, 1.96, 1.47. M_{78} are missing and are unknown in any specimen. These measurements and those for the upper molars given below differ slightly from the tooth lengths given by Simpson (1929: 92, 97) for the same specimens because of the additional preparation undertaken during the present study.

In occlusal view, the upper molars have an hour-glass outline, the long axis of which is set transversely in the maxilla (Fig. 2A). The lingual half of each molar is offset posteriorly from the buccal half, so that the long axis is actually obliquely transverse. Molars increase in length and width from M^1 to M^3 and thereafter decrease in both dimensions. As in the lower molar series, differences between upper molars are either proportional or are due to differential wear; the details of one molar may be taken as representative (Figs. 10-14). The maximum lengths and widths in millimeters of the molars of the holotype of *Docodon superus* (YPM 10647) are respectively: M^1, 1.76, 1.89; M^2, 2.02, 2.14; M^3, 2.14, 2.44; M^4, 2.02, 2.39; M^5, 1.68, 2.18.

Adjacent molars, both upper and lower, form a series of ridges and basins. Individual ridges are confined to a particular molar crown, whereas the basins are formed between two adjacent molars. In lower molars, one ridge runs longitudinally from front to back (cusp *a*, protoconid, p.c.c.) (Figs. 1D, 5). Another ridge transverses obliquely across the center (protoconid, m.i.c.c., p.i.c.c. in Figs. 1D, 5). These two ridges define anterior and posterior half-basins which, on every lower molar, are completely
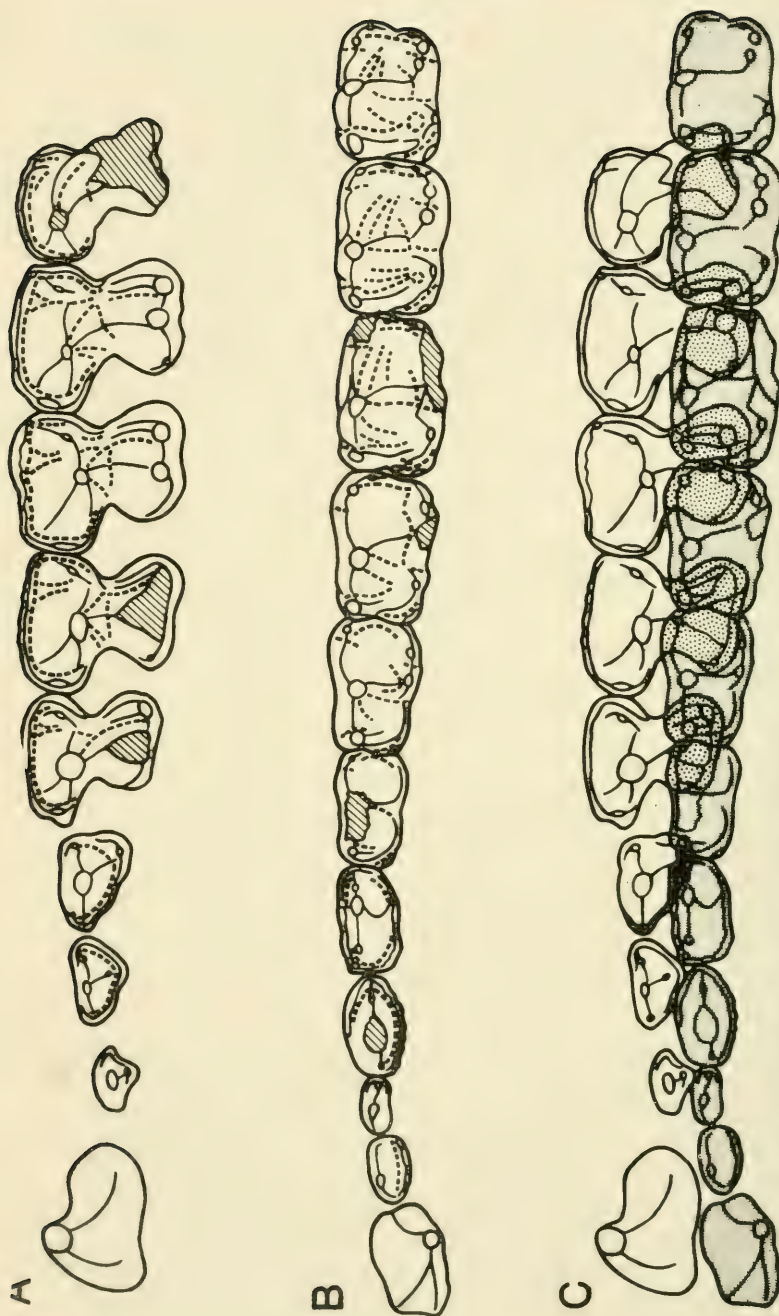
FIG. 2. Diagrammatic reconstructions of the dentition in *Docodon* in occlusal view. A) Upper right dentition (C^1 P^{1-3} M^{1-5}) based on *D. superus*, YPM 10647 and YPM 13769. B) Lower right dentition (C_1 P_{1-4} M_{1-6}) based on *D. victor*, YPM 11826. C) Occlusal reconstruction. Oblique hatching indicates damaged areas. Approximately ×10.

separated by the ridge from the protoconid to the middle internal cingulum cusp (m.i.c.c.). The anterior half-basin of one molar joins with the posterior half-basin of the preceding molar to form a large intermolar basin into which an upper molar occludes (Fig. 3, bottom). The upper molar is similarly arranged. A prominent ridge connecting the paracone and m.i.c.c. divides an anterior half-basin from a posterior half-basin (Fig. 1D). Adjacent half-basins form large intermolar basins; unlike the lower intermolar basins, however, the "floor" of these basins is not continuous (Fig. 2A).

OCCLUSION

The precise occlusal pattern in *Docodon* will remain uncertain until an associated upper and lower dentition are recovered. Without such complete material, it is nevertheless possible to approximate closely the occlusal pattern by carefully mapping the distribution of wear facets. More than 50 available specimens, representing single molars to nearly complete dentitions, provided the opportunity to determine the typical pattern of each facet.

Wear facets are designated by numbers (1-13 on lower molars, 14-21 on upper molars, Figs. 5-14). Areas of wear that are commonly represented by two or more confluent but differently oriented facets are given additional letter designations (e.g., 1a, 1b, etc.). The total pattern of facets is complex. Such a pattern could be produced only by rather specific facet-to-facet relationships; these are tabulated in Table 1. Facets that appear to have no opposing feature represent either normal abrasion of cusp apices (9a, 10, 14, 16a, 21) or very slight (and often uneven) wear on a cusp shoulder (15, 16b, 16c) as a result of the cusp apex penetrating abrasive food.

The facet-to-facet relationship given in Table 1 has been used to reconstruct the occlusion of a complete molar series (Fig. 2C). The details of molar occlusion are best illustrated in buccal, lingual, anterior and posterior views (Fig. 4). In buccal view (Fig. 4C-D), the buccal half of an upper molar shears past the protoconid-cusp *a* ridge. The lingual half of an upper molar occludes in the intermolar basin formed by two adjacent lower molars (Fig. 4A-B). However, the maximum anteroposterior length of the lingual half of an upper molar (x in Fig. 4A) is less
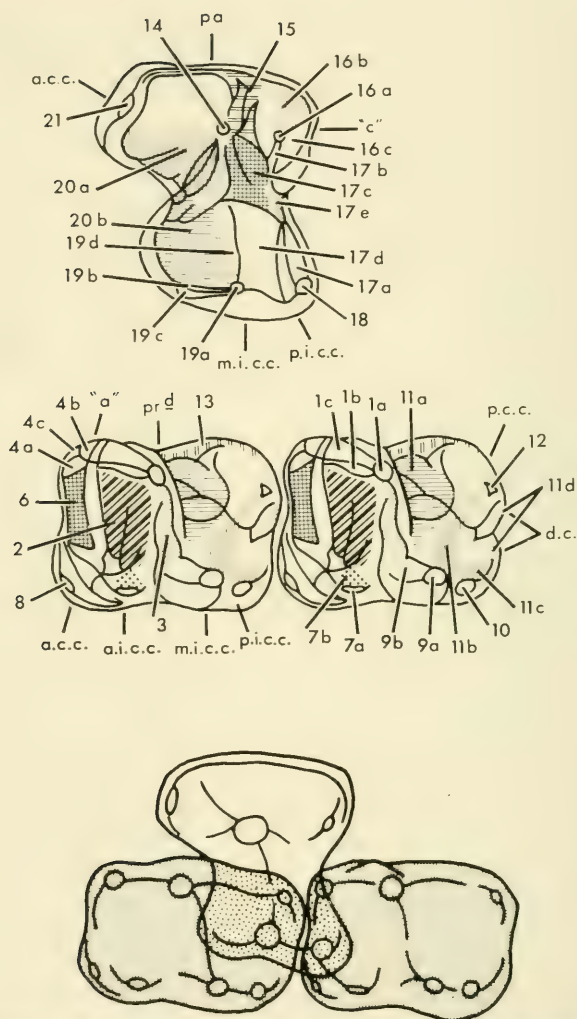
FIG. 3. Above, diagrammatic occlusal view of an upper and two lower molars to show the distribution of wear facets. Below, for comparison, the same molars in the approximate occlusal relationship required to produce the observed wear facets. See Table 1 for details of facet apposition.

than 3/4 the length of the lower intermolar basin (y in Fig. 4A). In actual distance on representative specimens, y - x is estimated to be about 0.5 mm. Therefore, this amount of movement of the lower dentition relative to the upper dentition may have been

TABLE 1. The reconstructed facet-to-facet relationships between typical lower and upper molars in *Docodon* sp.

Lower molar	Upper molar
1a	20b
1b, c	17b, c, e
2	17a
3	17a, 19b
4a, b, c	17b, c, d, e
5	17d
6	17a
17a, b	18
8	19a (18 in heavy wear)
9b	18
11a	19b, 20b
11b, c	19a, c
11d	19a, d
12 (variably developed)	19d
13	20a

Facets not directly associated with opposing facets: 9a, 10, 14, 16a and 21 represent a flattening abrasion of cusp apices by food and are apparently not formed by opposition with any other particular facets; 15, 16b and c are variably developed and represent slight wear around the apices of the paracone and upper cusp *c*.

possible. The relative proportions of certain facets also are evidence of anteroposterior movement. For example, only facet 17a is situated to appose facets 2 and 6; yet 17a is much narrower anteroposteriorly than 2 and 6, and therefore 2 and 6 must have moved anteroposteriorly relative to 17a to have produced the observed wear.

In anterior view (Fig. 4E-F), the lingual half of an upper molar is seen to shear down the posterior face of a protoconid at the same time as the paracone passes buccal to, and slightly behind, the protoconid. In active occlusion, the lingual, posterior and buccal aspects of the protoconid are in snug contact with an upper molar half-basin (Fig. 4F). The buccal half of the preceding upper molar shears across the buccal aspect of the protoconid and lower cusp *a* (Fig. 4G-H). In active occlusion, the anterior aspect of the protoconid and the entirety of lower cusp *a* contact the posterior half-basin of the preceding upper molar (Fig. 4H; the posterior half-basin of an upper molar is depicted in Fig. 4I).
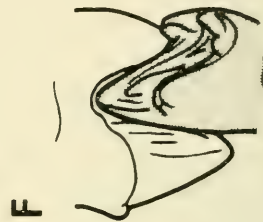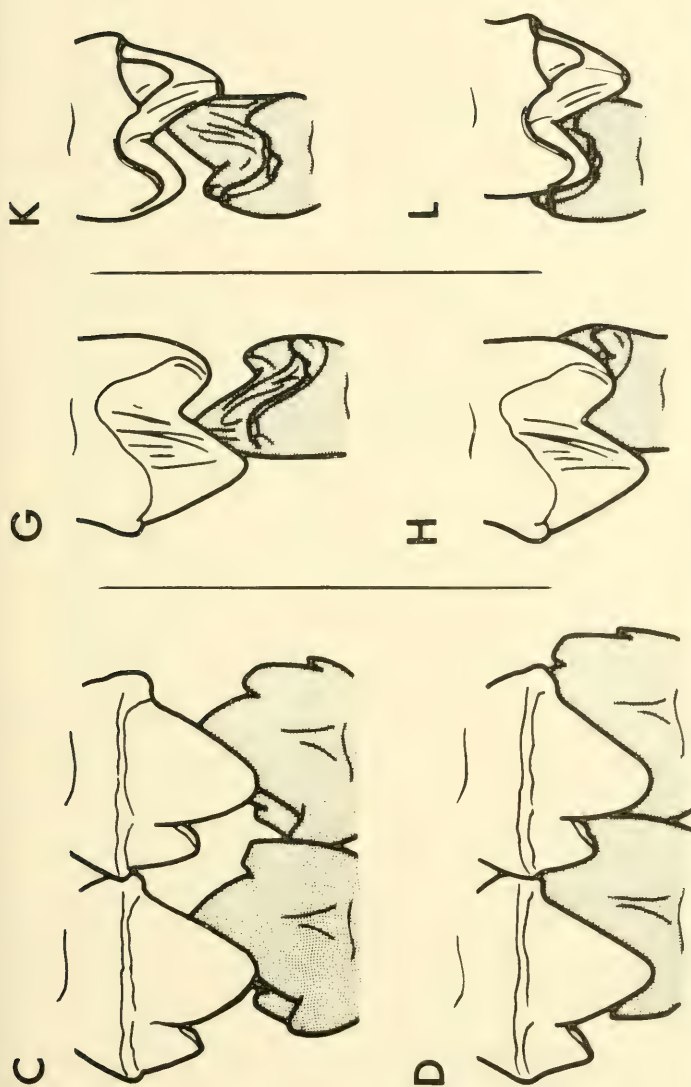
FIG. 4. Diagrammatic views of *Docodon* molars entering occlusion. A-B) Lingual view of $M^{2\cdot3}$ and $M_{3\cdot4}$; x, anteroposterior distance between upper molar facets that wear against lower molar facets separated by distance y. Thus the distance x minus y is an approximation of the amount of anteroposterior movement. C-D) Buccal view of the same. E-F) Anterior view of M^3 and M_3. G-H) Anterior view of M^2 and M_3. I-J) Posterior view of M^2 and M_3. K-L) Posterior view of M^3 and M_3.

In posterior view, the shear of an upper molar anterior and posterior to the buccal aspect of the protoconid is again evident (Fig. 4 I-J, K-L). In Fig. 4 I-J, the upper postero-internal cingulum cusp (p.i.c.c.) may be seen passing into the anterior half-basin of a lower molar. Likewise, in Fig. 4 K-L, the upper middle internal cingulum cusp (m.i.c.c.) passes into the posterior half-basin. Simultaneously, the crest between the paracone and upper m.i.c.c. shears against the posterior face of the protoconid.

FUNCTION

PREVIOUS OPINIONS. Simpson (1929: 85) briefly characterized the occlusal relationship in *Docodon* as "a premature and ill-fated effort toward the production of broad-crowned crushing or grinding teeth from the more ancient piercing insectivorous type". Later, Simpson (1933: 145) more explicitly expressed his opinion of the molar function in a discussion of the docodonts as a family within the order Pantotheria (a taxonomic assessment now abandoned by Simpson, 1959: 407, and other workers): ". . . the teeth have become quadrate, rather than triangular, the cusps are in general somewhat blunter and heavier, the shearing crests have disappeared as such, supplementary cusps have arisen, and the talonids have become relatively much larger and are well basined. There is conclusive structural evidence that these are related to the other pantotheres and merely represent a rather superficial specialization, but functionally they are very different. In the docodonts occlusion involves almost exclusively opposition [*vide infra*] . . . They may be considered as somewhat more durophagous than other pantotheres, but a more probable analogy seems to be with later forms, e.g., many bunodont primates, which are frugivorous-omnivorous. This end has been obtained in a way differing structurally from any later development."

Simpson (1933) also outlined four "general principles" or modes of occlusion: alternation, opposition, shearing and grinding. Opposing occlusion, the mode Simpson believed to have been employed by docodonts to the practical exclusion of any other, is achieved either by opposing "positive elements (cusps, crests) into negative elements (basins, valleys) . . . or positive elements against other positive elements". Simpson's discussion makes clear

his opinion that occlusion in *Docodon* was of the former type. In a later paper (1936: 946-947), he further noted that "opposition is also associated principally with orthal motion, but is generally also accompanied by some freedom of motion in a horizontal plane, propalinal or ectental . . . The function is in part grasping . . . but as a distinct type is primarily that of crushing". In the same paper (p. 952) he reiterated his view that the docodonts ". . . have emphasized opposition almost to the exclusion of shearing and alternation. . . ." Patterson (1956: 77), in his revised diagnosis for the order Docodonta which was originally proposed by Kretzoi (1946), concurred with Simpson, describing the molars as opposing and crushing.

INTERPRETATION OF THE PRESENT STUDY. The claim that *Docodon* molars are crushing teeth is apparently based on the relatively broad crowns (especially of the upper molars), the robust, often blunt cusps, the large, talonid-like basins, and the apparent lack of shearing crests. If its molars were specialized for crushing, *Docodon* would differ from other Mesozoic mammals in which shearing is the principal mode of occlusal action. Moreover, the occlusal diagram of *Docodon* (Fig. 2C) shows that a relatively large area of the upper molar crown overlaps, or opposes, the lower molar crown. This fact would appear to support the claim that *Docodon* molars crush and do not shear.

A complete evaluation of molar function in *Docodon* must take into account more than general morphology and a two-dimensional occlusal diagram. Three features of the *Docodon* dentition are pertinent to a functional interpretation: 1) the inclination of the prominent crests between cusps, 2) the orientation and relative size of wear facets, and 3) the distribution of crenelations (ribs and furrows) on the larger wear facets.

(1) Crests. The functional importance of crests that interconnect or otherwise define cusps has been widely recognized and has been recently re-emphasized by Mills (1966). Crests function as cutting or shearing blades. Their shearing efficiency is increased by an obliquity of the edge which is analogous in principle to a guillotine, as Mills has pointed out. In the *Docodon* dentition, oblique crests are prominent features. On lower molars (Figs. 5, 6 and 7) a substantial crest runs from the protoconid to the poste-

rior cingulum cusp (p.c.c.) and from the protoconid to the middle internal cingulum cusp (m.i.c.c.). Both crests are major sites of shear; wear facets are developed on both sides of each crest. Perhaps to a lesser extent the crest from the protoconid to cusp *a* (Figs. 6 and 7) is also a shearing crest. On upper molars (Figs. 10 and 12) the most prominent crest runs transversely across the crown from the paracone to the middle internal cingulum cusp (m.i.c.c.) (Figs. 10 and 12). Other crests descend anteriorly and posteriorly both from the paracone and middle internal cingulum cusp. The best defined of these descends anteriorly from m.i.c.c. and bears facets 19c and 19b (Fig. 12). This crest, together with the crest from the paracone to the m.i.c.c., bypasses a similar crest from the protoconid to the lower m.i.c.c. (Fig. 4E-F) and generates a major transverse shear. There is little doubt that these and other crests on *Docodon* molars are related to a cutting rather than a crushing mode.

(2) Facets. The orientation and relative sizes of molar facets are another indication of dental function in *Docodon*. The following graphical technique was used to obtain an estimate of the verticality and areal extent of facets. Each of the major facets was photographed in two views: one view perpendicular, the other view parallel to the plane of the wear facet. Tracing the facet on an enlarged perpendicular view with a planimeter yielded an estimate of the size of the facet. An enlarged parallel view yielded the orientation of the facet relative to a horizontal plane. On both upper and lower molars over 80% of the total facet area is oriented within 30° of the vertical — well within the range expected of shearing surfaces. Thus, as upper and lower molars occlude, the majority of wear facets are established by the shearing action of bypassing cusps and crests and not by contact of surfaces perpendicular to jaw movement. This interpretation assumes that mandibular movement in docodonts was primarily orthal. Such a supposition is reasonable. On better preserved mandibles a coronoid boss is evidence of transverse processes of the pterygoid that would restrict lateral movement. A small amount of anteroposterior movement is indicated by the wear facet relationships (see above). However, there is no evidence that a large amount of propalinal movement was involved. Instead, it seems likely that the lingual half of an upper molar may have occluded in two

slightly different positions — one just anterior to the other. If the lower intermolar basin was exactly the size of the lingual half of the upper molar, impacted food might block the full shearing stroke. To prevent this, the lower intermolar basin is slightly larger than the lingual half of the upper molar.

(3) Crenelations. A third aspect of the *Docodon* dentition is the presence of crenelations or ribs and furrows on the occlusal surface of the crown (Figs. 7-9, 12-14). These features were briefly mentioned by Marsh (1887), Butler (1939) and Patterson (1956); Simpson (1929: 91-92) described them in some detail but neither he nor any other author offered a functional explanation of them. Crenelations are most prominently developed on the larger facets (e.g., facets 2, 11a, 17c, 20a). These facets are produced by the shearing action of cusps or crests bypassing in close apposition. If these surfaces were simple flat facets, no additional shearing effect could be generated after a cusp or crest, acting as a blade, passed its counterpart on the opposing tooth. An appropriate analogy is a pair of scissors in which the cutting effect is exclusively confined to the point at which each blade
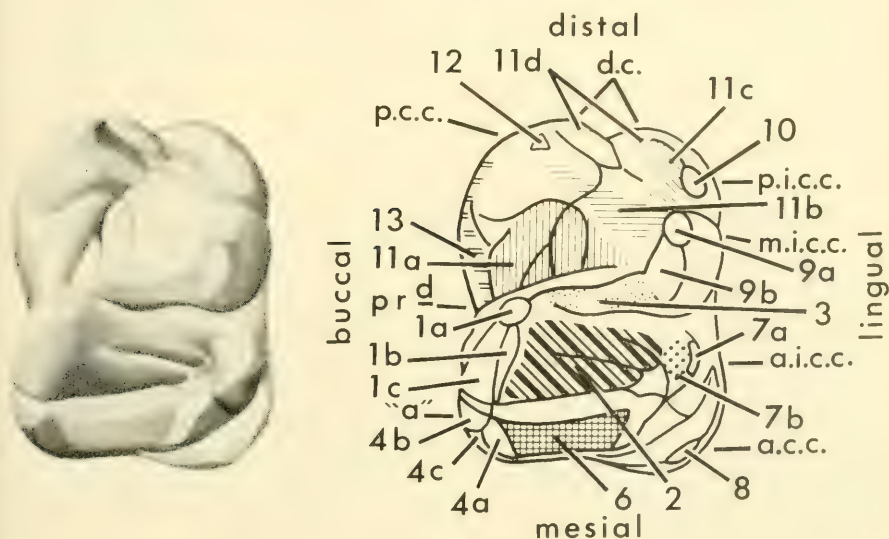

FIG. 5. Crown view of M_6 of *Docodon victor* (YPM 11826). ×23.5. See text and Table 1 for details of facets la through 21 in this figure and in Figs. 6-14, and see Fig. 1 for abbreviations.
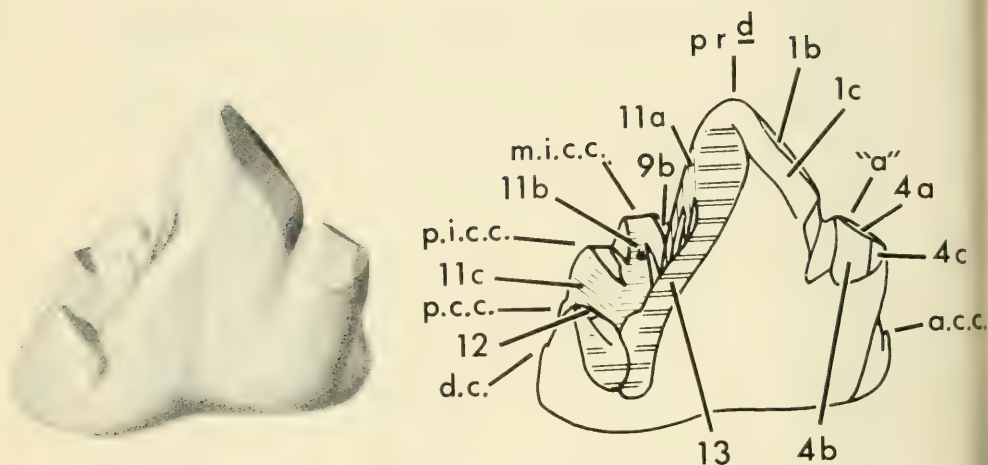
FIG. 6. Buccal view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

passes the other. Material between the flat sides of two scissors
blades cannot be cut. Crenelations in *Docodon* circumvent this
problem by acting as secondary shearing edges after primary
shearing edges (cusps, crests) have bypassed their counterparts.
Two factors account for this additional shearing effect. First, the
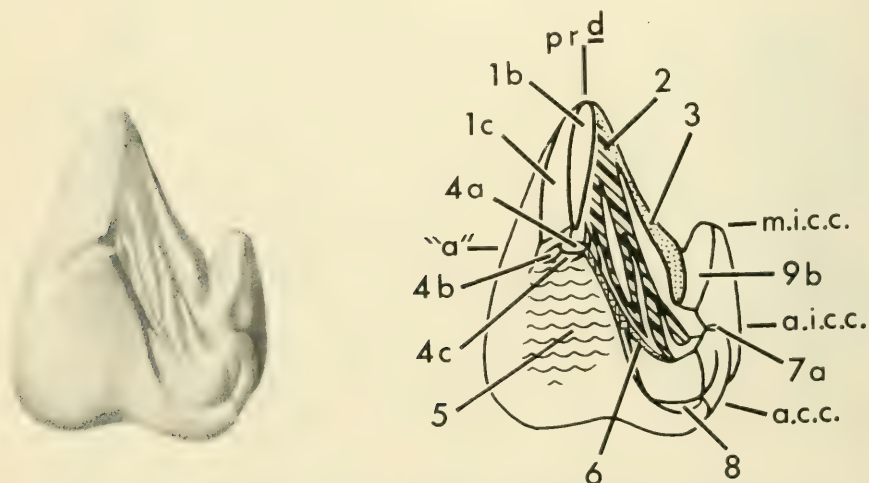force per unit area of occlusal surface is concentrated on the

FIG. 7. Anterior view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

linear crenelations by the recessing of the surfaces between them. Second, the beveling of the tops of the crenelations produces sharp edges (Fig. 15). Food brought to bear against these edges will tend to be sliced by these edges, although the cutting action here is in no measure as complete as between the major crests and cusps.
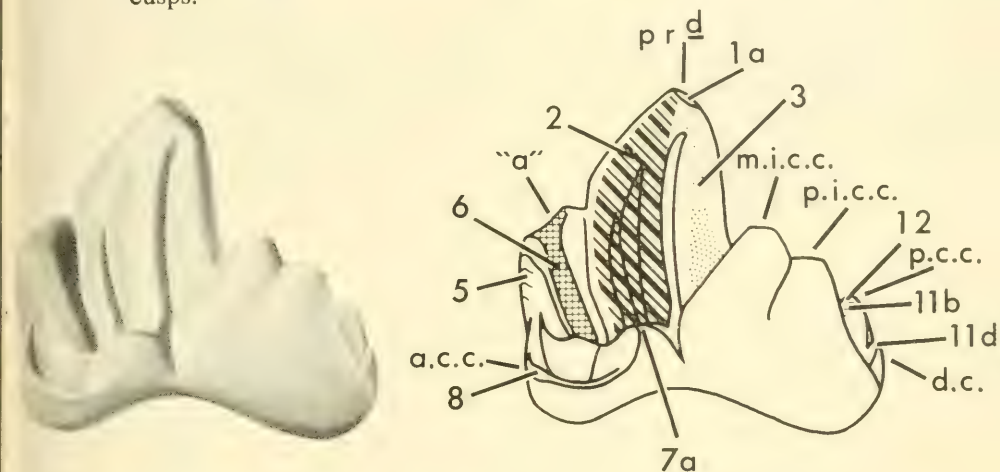

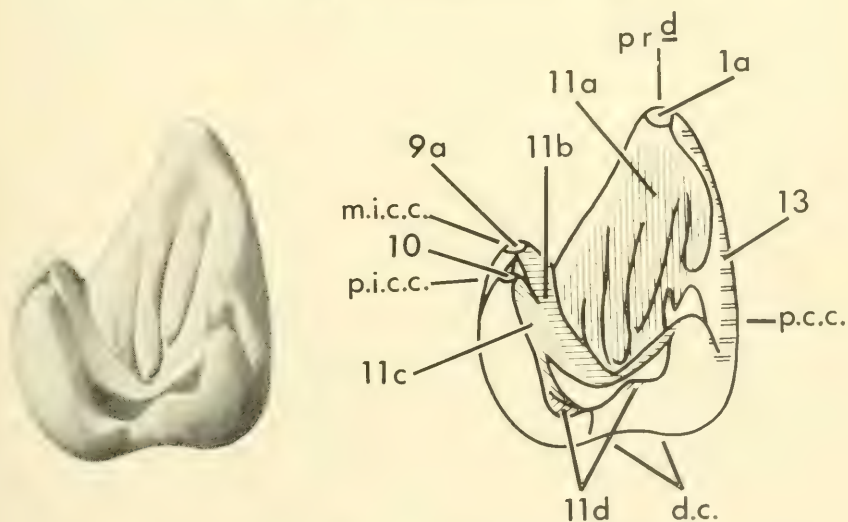FIG. 8. Lingual view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

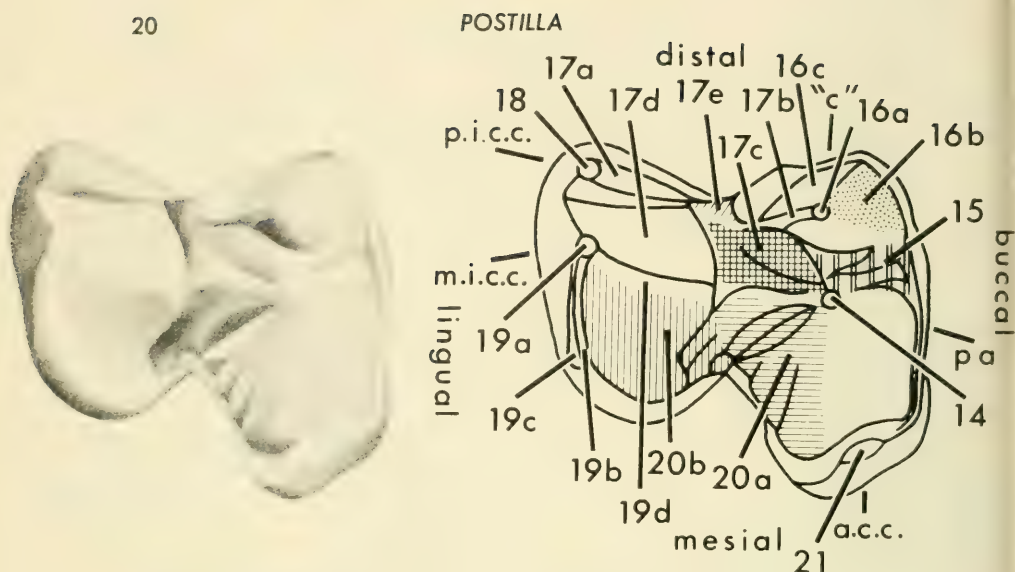FIG. 9. Posterior view of M_6 of *Docodon victor* (YPM 11826). ×23.5.

FIG. 10. Crown view of M³ of *Docodon superus* (YPM 10647). ×21.5.

DISCUSSION

On the basis of the morphology of the molar crowns, the orientation of wear facets, and the presence of accessory shearing crenelations, the dentition of *Docodon* is more appropriately characterized as functionally shearing rather than crushing. I doubt that opposing and crushing (in the sense of Simpson, 1933) is an efficient method of masticating most types of plant and animal food. In molluscivorous species, for example, crushing dentitions are obviously required to break into shells. Aside from such specialized diets involving very hard and brittle material, all other food sources involve material that is pliable to some degree. The most efficient method to reduce pliable material for ingestion and digestion would appear to be fragmentation by shearing. Thus shearing is probably the most important functional principle in the majority of mammalian dentitions. The diversity of molar form among mammals represents not so much a diversity of functional modes, but a diversity in the manner in which a shearing mode can be specifically adapted to various types of food.

The evolution of the *Eozostrodon — Haldanodon — Docodon* lineage, as interpreted by Crompton and Jenkins (1968), represented an adaptive shift from a simple longitudinal shear to a

FIG. 11. Buccal view of M³ of *Docodon superus* (YPM 10647). ×21.5.

complex pattern of both longitudinal and transverse shear. The *Docodon* lineage exploited the expansion of lingual cingula to produce additional shearing surfaces. These surfaces represent a proportionately larger total occlusal area than could be developed by the simple longitudinal shear of *Eozostrodon* and related eozostrodontids. This development is perhaps related to the increase in molar number of *Docodon* over that in eozostrodontids. In the latter, the amount of shearing surface was more or less proportional to molar length. In docodonts, however, with the lingual expansion of the molar crowns and the addition of transverse
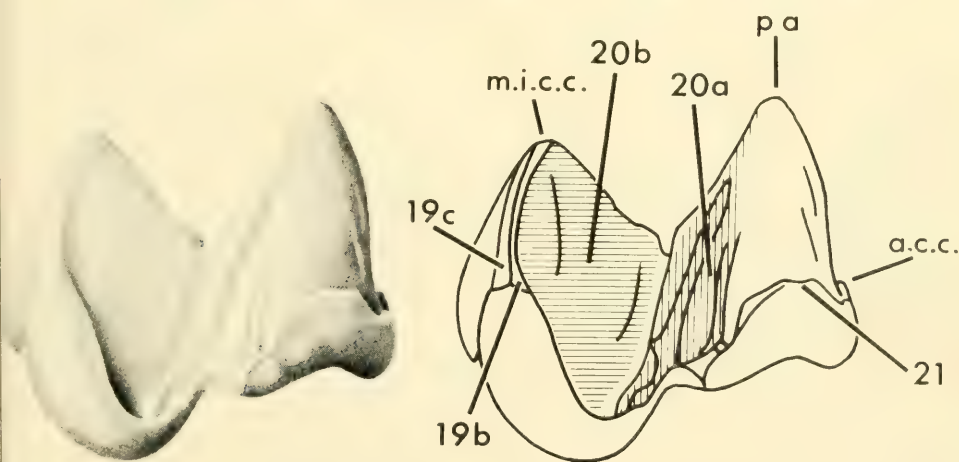

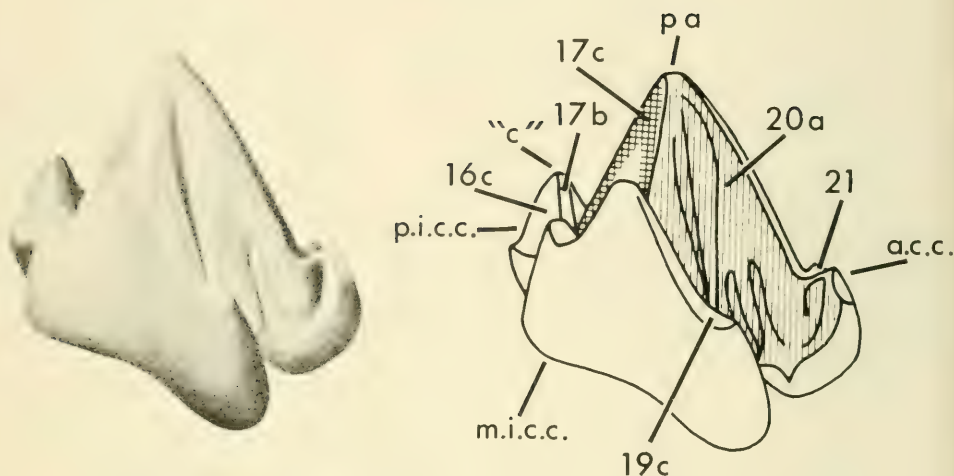FIG. 12. Anterior view of M³ of *Docodon superus* (YPM 10647). ×21.5.

FIG. 13. Lingual view of M³ of *Docodon superus* (YPM 10647). ×21.5.

shearing surfaces, the amount of shearing surface was less depen-
dent on molar length. Thus the *Eozostrodon* — *Docodon* lineage
appears to have increased the total molar shearing surface by both
increasing the number of molars and by expanding the shearing
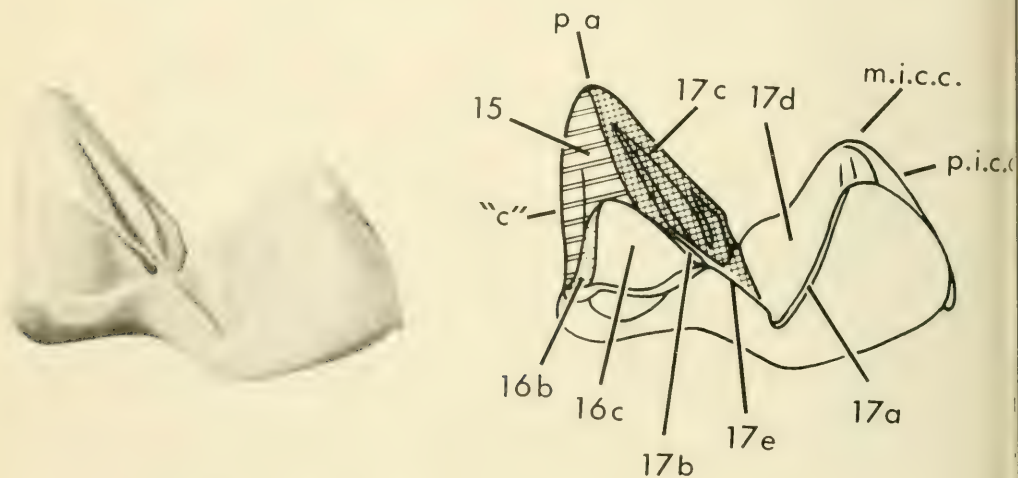features on each molar.

FIG. 14. Posterior view of M³ of *Docodon superus* (YPM 10647). ×21.5.

FIG. 15. Stereoscopic photographs of M_5 of *Docodon victor* (YPM 11826) in posterior view to show the sharp ridges resulting from the beveling of the vertical crenelations. The buccal aspect of the postero-internal cingulum cusp has been lost.

ACKNOWLEDGEMENTS

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